

**BIOLOGY OF FOUR SPECIES OF *NOTIPHILA* FALLÉN (DIPTERA:
EPHYDRIDAE) ASSOCIATED WITH THE YELLOW WATER LILY,
NUPHAR LUTEUM (NYMPHAEACEAE)**

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Abstract:—The life histories of four species of *Notiphila*, *N. bella*, *N. eleomyia*, *N. kentensis*, and *N. nudipes*, that feed on anaerobic sediments surrounding roots of the yellow waterlily, *Nuphar luteum*, are described. Males of *N. eleomyia* and *N. nudipes* form mating aggregations resembling leks on flower buds, flowers, fruits, and occasionally leaves of the host plant, and mating occurs within these aggregations. Females deposit large clusters of eggs on these plant parts, particularly the flowers and fruits. The incubation period lasts 4–6 days, and newly hatched larvae drop off the egg masses and fall into the underlying sediments where they feed during the summer and fall months. Overwintering occurs as nearly mature larvae. In late May and early June, larvae move to roots of *Nuphar* and insert their spiracular spines into air spaces within the root tissue. The pupal period lasts 14–22 days. *Notiphila bella* is univoltine, but the three other species may be bivoltine. Information is presented on the utilization of wetland plants by different species of *Notiphila*, and it is proposed that speciation and adaptive radiation involved movement onto these different “host plants” for the purpose of obtaining oxygen by the larvae.

Key Words: Shore flies, *Notiphila*, Ephydridae, Diptera, *Nuphar*, Ohio

Wetlands subjected to long-term inundation develop anaerobic conditions in the underlying soils (Mitsch and Gosselink 1992). As a result, plants and animals living in such anaerobic conditions must acquire a variety of mechanisms that allow them to acquire the oxygen necessary for their metabolic functions. Many wetland plants possess aerenchyma in their stems, rhizomes, and roots that allows for the diffusion or mass transport of oxygen from the photosynthesizing aerial portions of the plant to the roots (Armstrong 1964, 1978; Dacey 1980, 1981; Grosse and Mevi-Schutz 1987; Mevi-Schutz and Grobe 1988). Larvae of some insects living in anaerobic soils have

modified posterior spiracles that form elongate spines that can be inserted into the aerenchymatous tissues of plants and thus acquire oxygen (Müller 1922; Varley 1937, 1939; Keilin 1944; Hinton 1953, 1968; Hartley 1958; Houlihan 1969a, 1969b). A large and widely distributed taxon having this ability are shore flies belonging to the genus *Notiphila* Fallén.

The genus *Notiphila* is worldwide in distribution, occurs in a variety of wetland habitats, and is speciose, with 53 species having been recorded from America north of Mexico (Mathis 1979, Wirth et al. 1987). Meaningful biological studies are available for only five of these Nearctic species, al-

though fragmentary information has been published for an additional 15. Berg (1950) reared *N. (Notiphila) loewi* Cresson from anaerobic soils surrounding the rhizomes and roots of pondweeds (*Potamogeton* spp.). Eastin and Foote (1971) discussed the natural history of *N. (Dichaeta) caudata* Fallén, a species that is unusual within the genus in that its larvae are not buried in anaerobic sediments but crawl about on the surface. Larvae of this species lack spiracular spines. Busacca and Foote (1978) presented life history observations on two species, *N. (Agrolimna) aenigma* Cresson, and *N. (N.) solita* Walker, that obtain oxygen from roots of cattails (*Typha latifolia* L.). They also described the eggs, larvae, and puparia of these two species. Deonier et al. (1978) described the immature stages and outlined the natural history of *N. (N.) carinata* Loew, a species that is associated with water willow (*Justicia americana* (L.) Vahl.) growing in slow-flowing streams in southwestern Ohio and other regions east of the Mississippi River.

Some biological observations and indications of association with particular wetland plants are also available for *N. (N.) bella* Loew, *N. (N.) eleomyia* Mathis, *N. (N.) kentensis* Huryn, *N. (N.) mathisi* Huryn, *N. (N.) nudipes* Cresson, *N. (N.) paurooura* Mathis, *N. (N.) poliosoma* Mathis, *N. (N.) shewelli* Mathis, *N. (N.) taenia* Mathis, *N. (N.) theonae* Huryn, and *N. (A.) deonieri* Mathis, *N. (A.) olivacea* Cresson, *N. (A.) quadrisetosa* Thomson, *N. (A.) scalaris* Loew and *N. (A.) scoliochaeta* Mathis (Mathis 1979; Todd and Foote 1987; Huryn 1984, 1987).

In this paper, we present observations of the natural history of *Notiphila bella*, *N. eleomyia*, *N. kentensis*, and *N. nudipes* occurring in stands of the yellow water lily, *Nuphar leuteum* (L.) Sibth. and J. E. Smith. We also discuss resource partitioning in the genus *Notiphila* and propose a possible mode of speciation within this taxon.

MATERIALS AND METHODS

Site description.—Two marshes located in Portage County in northeastern Ohio (Fig. 1) were sampled in this study. The larger marsh is situated on the east side of State Highway 43, 9.3 km north of the northern city limits of Kent. The marsh is bordered on the west by the highway, residential property on the north, and open lowland woodlands on the east and south. The emergent marsh vegetation consists of species of *Carex*, *Typha*, and *Sparganium* around the perimeter, a large stand of *Typha* and *Sparganium* growing intermixed on a floating mat of dead vegetation at the east end, and a large stand (ca. 2700 m²) of yellow water lily at the west end (Fig. 2). In addition to the emergent vegetation, there are thick growths of floating duckweeds, *Lemna minor* L., *Wolffia punctata* Griseb., *Spirodela polyrhiza* (L.) Schleid., and water milfoil, *Myriophyllum exalbescens* Fernald. The marsh is persistent and has a rather stable water level. The water depth varied from 50 to 80 cm during the two-year study period.

The second, much smaller marsh is located 0.8 km east of the Kent State University main campus, between Horning Road and U.S. Highway 261 (Fig. 3). It is bordered by Horning Road on the west, residential property and a pond on the north, Highway 261 on the east, and an abandoned agricultural field on the south. The vegetation is more diverse than in the larger marsh and consists of discontinuous stands of *Typha*, *Carex*, *Phalaris*, *Sparganium*, *Eleocharis*, and *Nuphar*. At the time this marsh was characterized by Todd and Foote (1987), the *Nuphar* stand encompassed some 1157 m², but low water levels since that survey has permitted *Typha* to invade. As a result, the continuous stand of *Nuphar* in 1995 is only some 100 m², and the water depth averages only 10 cm.

Sampling methods for adults.—A transect was established across the center of the *Nuphar* stand at the Route 43 marsh (Fig.

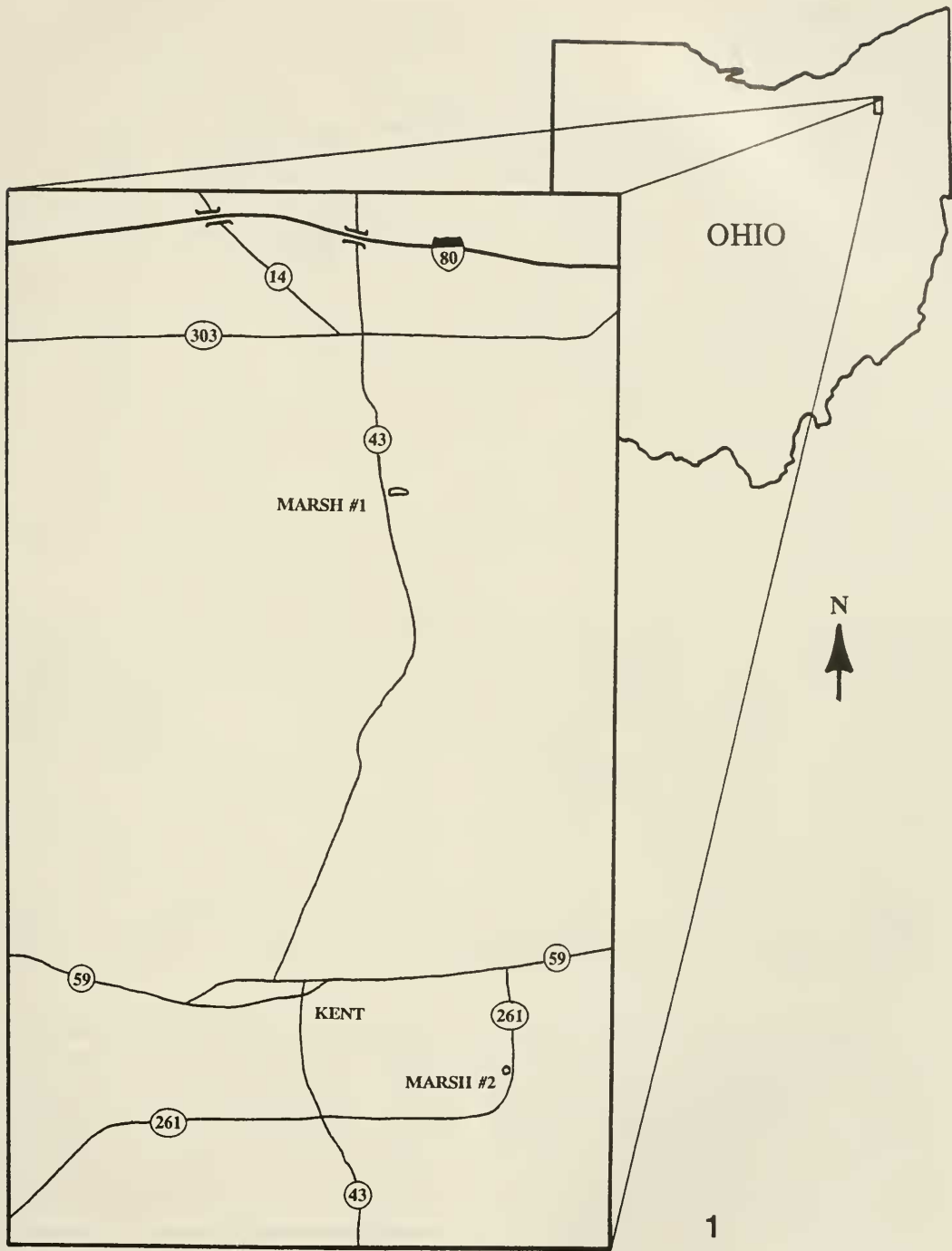
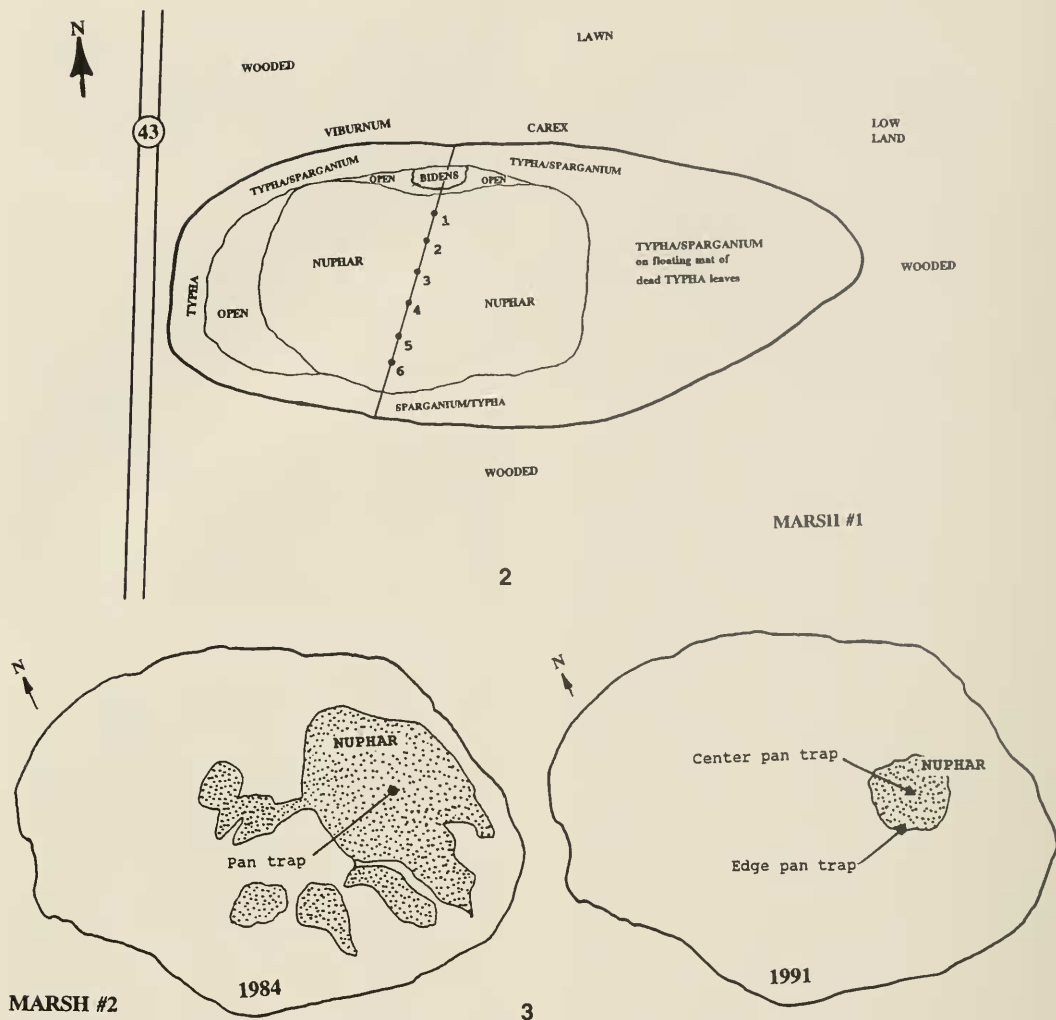


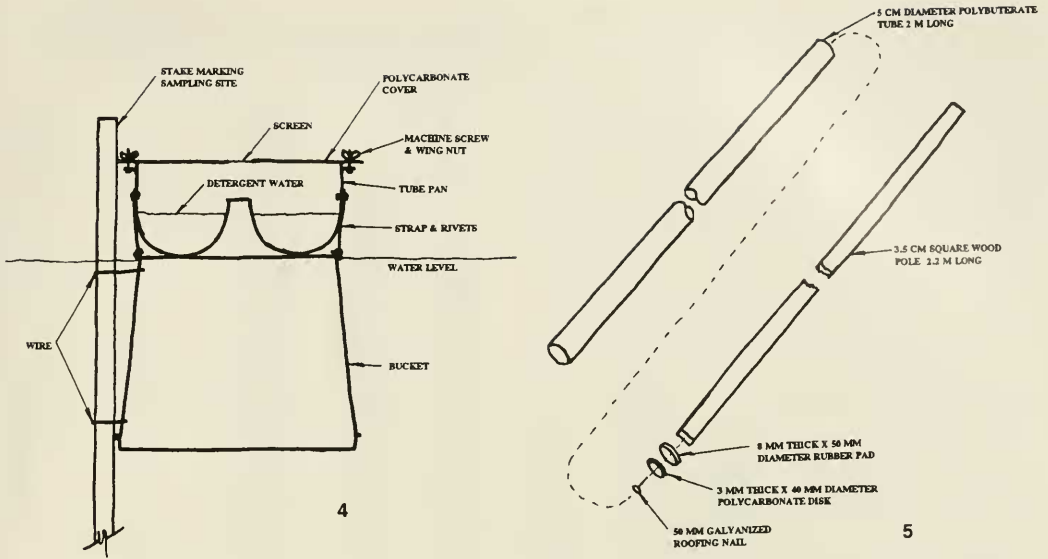
Fig. 1. Map showing locations of two study marshes in northeastern Ohio.



Figs. 2-3. 2, Map of the Route 43 marsh showing stands of vegetation. 3, Map of Horning Road marsh showing stands of *Nuphar luteum*.

2). The transect extended south-southeast from the north edge of the marsh. A rope, 65 m long, that was attached at each end of the transect completely crossed the width of the marsh. The *Nuphar* stand along the transect was 45 m wide. Six sampling sites were established along the transect at 6 m intervals. Each site was marked by wooden stakes that encompassed a 4×2 m plot. Two sampling sites were established in the Horning Road marsh (Fig. 3). One of these was in the center of the *Nuphar* stand, the other some 5 m distant where *Nuphar* and *Typha* were intermixed.

Collections of adult *Notiphila* were taken weekly at 2 locations in each marsh between early June and early October from 1991 to 1993. All collections were made during the same 24 hour period using identical detergent pan traps (Southwood, 1978). The pan traps consisted of white polyethylene storage containers measuring $30 \times 15 \times 10$ cm. Each trap contained approximately 50 ml of water into which one ml of dishwashing detergent had been added. All traps were placed in the marshes during the mid-afternoon and collected 24 hours later. In the Route 43 marsh, traps



Figs. 4–5. 4, Emergence trap, cross-section diagram. 5, Diagram of core sampling device.

were placed at sampling sites 1 and 3, whereas in the Horning Road marsh, they were placed at both collecting sites. The contents of the traps were returned to the laboratory where the adult *Notiphila* were removed, identified, sexed, and counted.

Collections of adult *Notiphila* from the unopened buds or flowers of the *Nuphar* were obtained either by using a modified battery-operated hand vacuum (Marshall 1982) or by carefully placing a large polyethylene bag over the buds or flowers and then breaking off the peduncle below the water surface and sealing the bag.

During the summer of 1992, six emergence traps were placed along the transect in the Route 43 marsh, one trap at each end of the sample plots. The traps were constructed by attaching a one-piece plastic tube pan to the outside bottom of a plastic 3-gallon (11.25 L) bucket (Fig. 4). Prior to attaching the pan, a small hole was cut in the center of the bucket. A lid of clear, polycarbonate plastic was attached to the bucket with machine screws and wing nuts. A 5 cm vent hole was cut in the center of the lid and covered with plastic window screening. The two holes allowed for vent-

ing but prevented rainwater from flooding the trap. Traps were attached to the wooden stakes delimiting the sample plots and the bucket part of each trap was completely submerged. Each tube pan contained approximately 500 ml of water and one ml of detergent. The traps were emptied weekly between June 15 and July 27, 1992, and the *Notiphila* identified, sexed, and counted.

Sampling methods for larvae.—Core samples of the bottom substrates were taken at the sample sites in the Route 43 marsh on September 20, 1991 (site 1), February 18, September 25, October 8, 1992, and April 6, 1993 (all six sites). Cores were obtained using a 5 cm colorless, polybuterate tube that was 2 m long (Fig. 5). A piston fitted into the coring tube allowed the substrate to be sampled without being flooded by the overlying water. Cores were placed in polyethylene bags and returned to the laboratory where they were examined for *Notiphila* larvae. Larvae were extracted from the cores either by using an elutriator similar to that described by Whitman et al. (1983) or adding water to the mud sample to reduce it to a slurry that was then spread

over the bottom of a large tray and inspected visually.

Rearing methods.—Portions of *Nuphar* rhizomes and attached roots were removed from the marsh substrate at various times throughout the year and examined visually in the laboratory for attached larvae and/or puparia. Puparia were carefully removed from the roots and placed on moist sphagnum moss in test tubes (Berg 1950). They were oriented in the moss so that the posterior spiracular spines of the puparia were exposed to air. No attempt was made to rear larvae.

Identification of adults.—Males were determined by using keys of Mathis (1979) and Huryn (1987). Tentatively determined specimens of each species were submitted to Wayne Mathis at the Smithsonian Institution for confirmation.

RESULTS OF TRAPPING IN THE TWO MARSHES

Pan trapping in the Route 43 marsh.—Approximately 53,200 adult *Notiphila* of eight species (Table 1, Fig. 6) were obtained in the detergent pan traps during the three-year survey. Of these, 10,620 (20.4%) were males. Three species, *N. eleomyia*, *N. kentensis*, and *N. nudipes* dominated throughout the study (Figs. 7–9), representing 95.2% of the total number collected. These three, plus *N. bella*, constituted over 97% of the males collected. *N. eleomyia* was the most abundant species, accounting for 60.3% of the total number. The second most abundant species was *N. kentensis*, accounting for 25.5% of the males collected, whereas *N. nudipes* accounted for only 9.4% of the males identified. *Notiphila bella* was present only during late spring and early summer and commonly was the first species to emerge (Fig. 10). Four other species, *N. olivacea*, *N. pauroura* Mathis, *N. solita*, and *N. taenia*, were only collected sporadically. *Notiphila taenia* was taken predominantly from mid to late June, although a few were taken as late as October.

Table 1. Temporal distribution of adults of all species of *Notiphila* collected in two marshes in Portage County, Ohio.

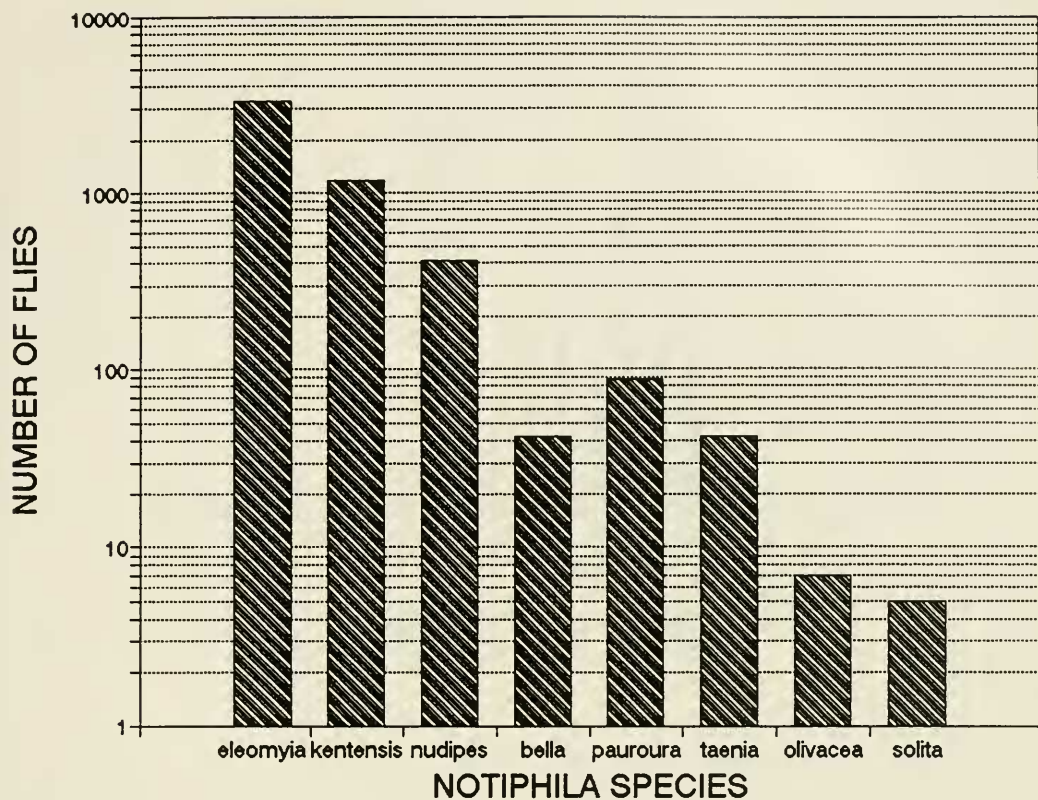
Week number	Route 43 marsh			Hornig Road marsh 1991
	1991	1992	1993	
19	*	*	—	*
20	*	*	—	*
21	*	*	41	*
22	*	*	544	*
23	*	1451	3898	*
24	*	4309	10,410	*
25	2850	2052	8864	254
26	1925	1370	3524	79
27	1056	3316	*	66
28	381	*	*	4
29	233	2322	*	2
30	131	617	*	3
31	122	337	*	—
32	440	160	*	—
33	219	174	*	—
34	*	95	*	*
35	66	372	*	—
36	58	338	*	—
37	50	*	*	—
38	8	131	*	—
39	2	67	*	—
40	24	*	*	—
41	*	*	*	*
42	*	116	*	*
Totals	7565	17,386	27,274	408

* No collections made.

The other three species were taken irregularly throughout the summer months.

Forty-nine percent of the adults were taken in pan traps located near the center of the *Nuphar* stand (site 3), and 51% from the edge of the stand (site 1) (Fig. 11). The only species that did not follow this distributional pattern was *N. pauroura*, as only 25% of its adults were taken in the center-most traps.

The species composition of *Notiphila* remained fairly stable over the three years, but abundances changed considerably. The total number of individuals collected in 1991 was 7565, but this increased every year to the 27,275 trapped in 1993 (Fig. 12). The maximum number of flies trapped over a 24-hour period (Fig. 12) occurred



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Fig. 6. Total number of *Notiphila* males collected in the Route 43 marsh during 1992.

within days of the same date on all three years, VI-19-91, VI-17-92, and VI-16-93.

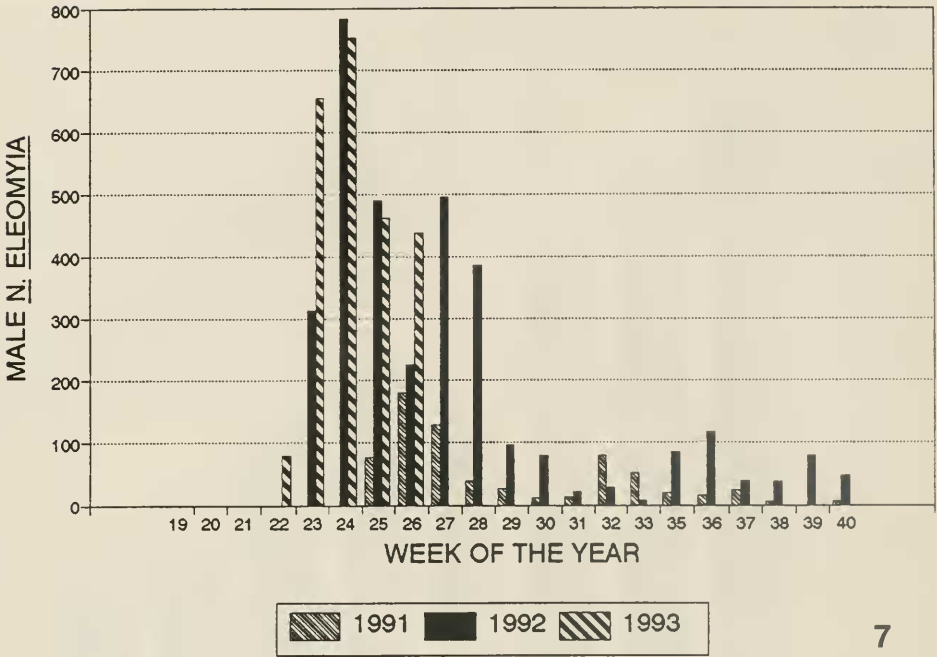
Pan trapping in the Horning Road marsh.—Only 408 adults (38.2% males) of five species of *Notiphila* were taken in the Horning Rd. marsh during the year-long survey (Table 1). The relative abundances of the five species were somewhat different than those obtained in the larger marsh. *Notiphila eleomyia* and *N. kentensis* accounted for 51.9% and 20.5%, respectively, of the adults trapped. However, the third most abundant species was *N. pauroura*, accounting for 13.5%, followed by *N. nudipes* (11.5%) and *N. olivacea* (2.6%).

Emergence traps.—Somewhat surprisingly, only nine males and 15 females of three species, *N. eleomyia* (5), *N. nudipes* (3), and *N. bella* (1), were collected in the

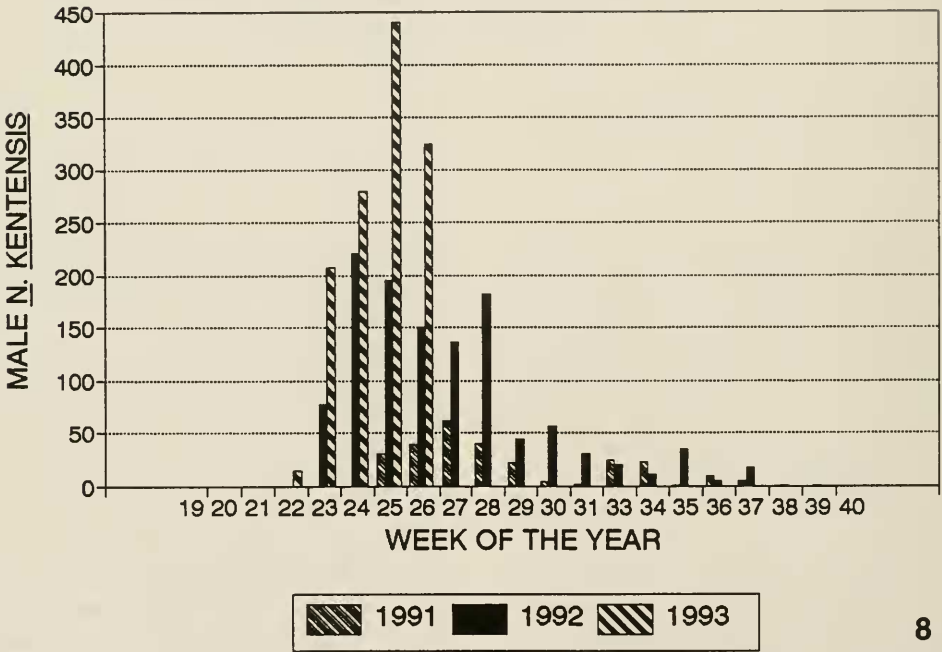
emergence traps. All appeared between VI-17 and VI-29-92. Most of the adults were taken at site 1, and none was taken in the trap at site 4.

Core sampling.—Twenty *Notiphila* larvae, all third instar, were extracted from the core samples of mud that were taken intermittently in the marshes (Table 2). No larvae were reared to the adult stage, so species identification was not possible.

Rhizome and root sampling.—A total of 229 larvae and 91 puparia were collected from samples of *Nuphar* rhizomes and roots (Table 3). All of the larvae were found during the late fall and early spring months in mud adhering to the rhizomes and roots. In contrast, all puparia were firmly affixed to the primary roots of the rhizomes and roots (Fig. 21) and were found only during late

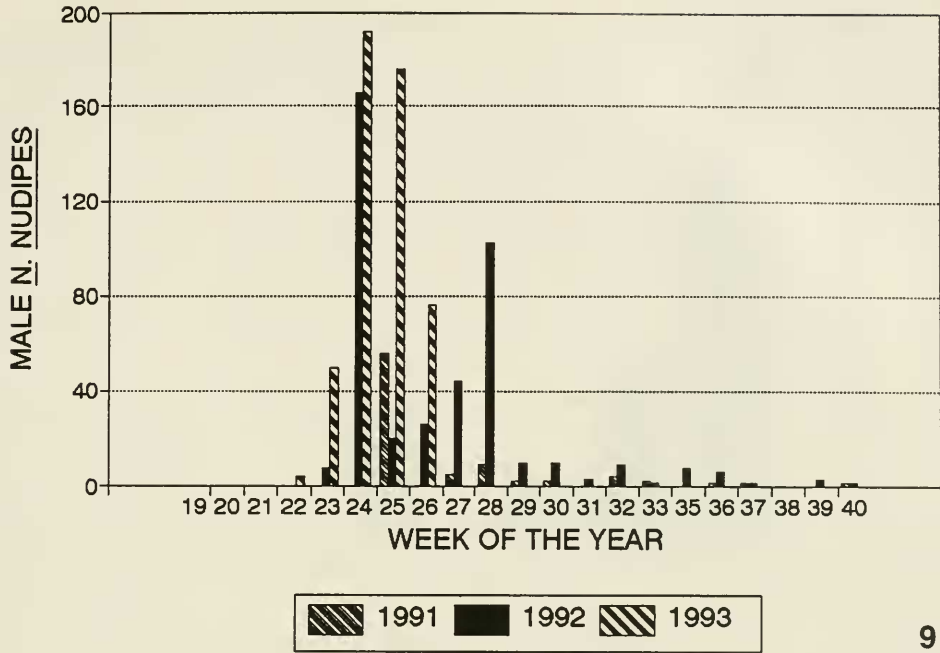


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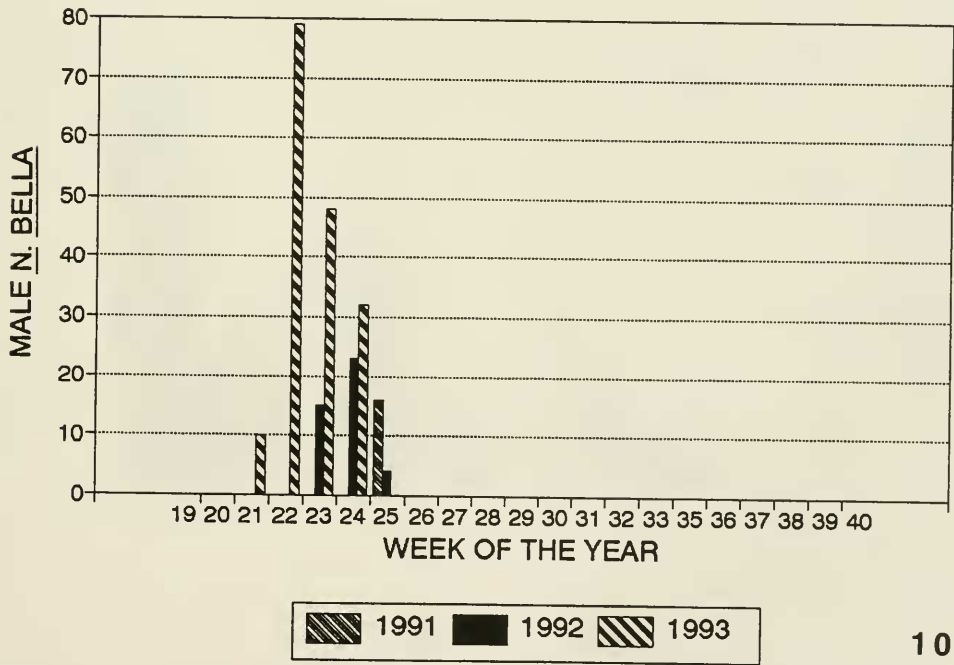


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Figs. 7–8. 7, Seasonal distribution of *Notiphila eleomyia* in the Route 43 marsh. 8, Seasonal distribution of *N. kentensis* in Route 43 marsh.

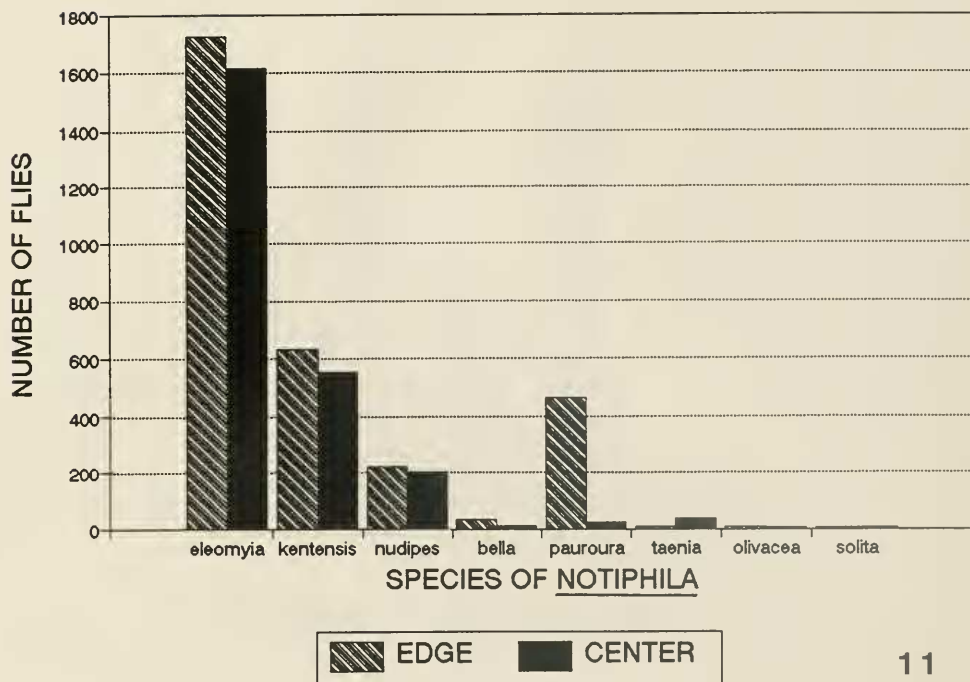


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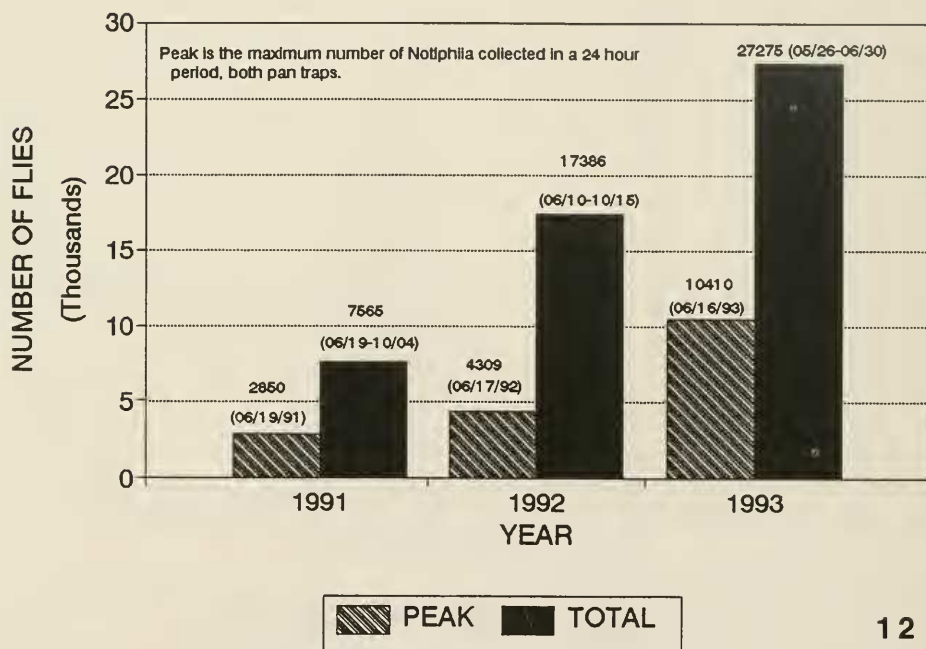


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Figs. 9–10. 9, Seasonal distribution of adult *Notiphila nudipes* in the Route 43 marsh. 10, Seasonal distribution of adult *Notiphila bella* in the Route 43 marsh.



11



12

Figs. 11–12. 11, Spatial distribution of adult *Notiphila* in the Route 43 marsh during 1992. 12, Total number of *Notiphila* collected in the Route 43 marsh between 1991 and 1993.

Table 2. Larvae collected in core samples taken at the Route 43 marsh in Portage County, Ohio.

Date	Site 1	Site 2	Site 3	Site 4	Site 5	Site 6
09/20/91	9	*	*	*	*	*
02/18/92	3	0	0	0	0	0
09/25/92	2	0	1	0	0	0
10/08/92	1	0	1	0	0	0
04/06/93	2	0	0	0	1	0
Totals	17	0	2	0	1	0

* Not sampled.

May and early June. Frequently, several puparia were attached to the same primary root, and there appeared to be a preference for the smaller roots located near the apical end of the rhizome. Some 20 puparia found on 10 roots of a single rhizome were all on roots that measured from 1.1 to 2.8 mm in diameter at the point where the root attached to the rhizome.

ADULT BEHAVIOR

The adult behavior of the species studied in this investigation resembled that described for other species of *Notiphila* by Busacca and Foote (1978), Deonier et al. (1978), Simpson (1976) and Van der Velde and Brock (1980). Adults spent most of their time walking over the surfaces of the *Nuphar* leaves and stems. They flew only a few centimeters when disturbed. While on the leaves, adults frequently paused to “taste” the surface, feeding on a microflora or absorbing the abundant honeydew deposited by a large leafhopper (Homoptera: Delphacidae) population. They were also observed to feed on bird droppings.

Courtship and Mating Behavior.—The flower buds, expanded flowers, and fruits of *Nuphar* were sites of a courtship aggregation of males that resembled lekking (Höglund and Alatalo, 1995). Large numbers of males, usually of a single species, distributed themselves rather evenly over the flower (Fig. 13) or bud (Fig. 14). They faced downward towards the water surface and held their wings out approximately 30 degrees from the centerline of the body,

Table 3. Number of *Notiphila* taken from roots of *Nuphar luteum* at the Route 43 marsh.

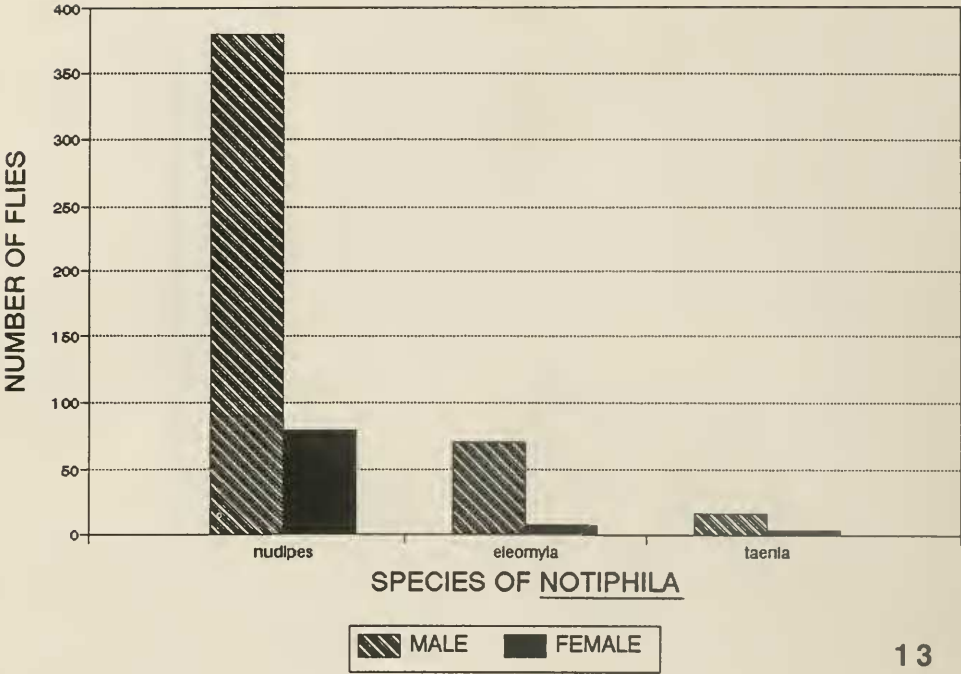
Date		Site 2	Site 4	Site 6
09/20/91	Larvae	5	*	*
	Puparia	0	*	*
05/28/92	Larvae	1	1	1
	Puparia	49	0	14
06/03/92	Larvae	0	*	*
	Puparia	21	*	*
04/06/93	Larvae	122	57	4
	Puparia	0	0	0
04/27/93	Larvae	26	6	13
	Puparia	3	0	0

* Not sampled.

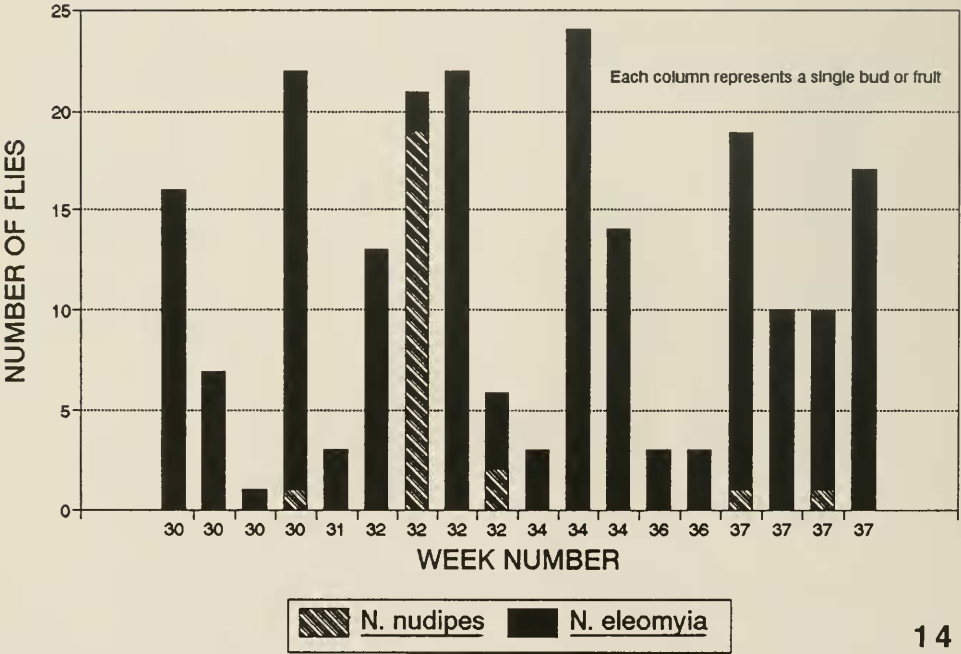
forming a v-shape (Fig. 15). Males constantly jostled each other and maintained a fairly uniform spacing. Whenever an interloper landed on the flower, it was quickly pounced upon by the nearby flies. If the newcomer was a male, he joined the group after a bit of shuffling to accommodate him. If the visitor was a female, there was a struggle among the males for her attention until one individual was able to copulate with her. Once the female was mounted, the other males resumed their positions on the flower head and ignored the mating pair. Occasionally, a male attempted to disrupt the mating pair, but these efforts were usually unsuccessful.

Males were particularly attracted to flowers that possessed numerous *Notiphila* eggs. Of male aggregations on 29 flowers, 16 flower buds, and two fruits that were examined, all but one possessed eggs (Fig. 16). On one occasion, an aggregation of six males of *N. eleomyia* was observed on a leaf that supported 775 eggs (Fig. 17).

Aggregations were observed in *N. eleomyia* and *N. nudipes* but not in *N. bella*, *N. kentensis*, or *N. taenia*. Mating behavior in those 3 species remains unknown. Male aggregations of *N. nudipes* typically were on the expanded flowers (418 of 488 males collected on flowers were of this species), whereas males of *N. eleomyia* were more commonly found on the buds (119 of 223

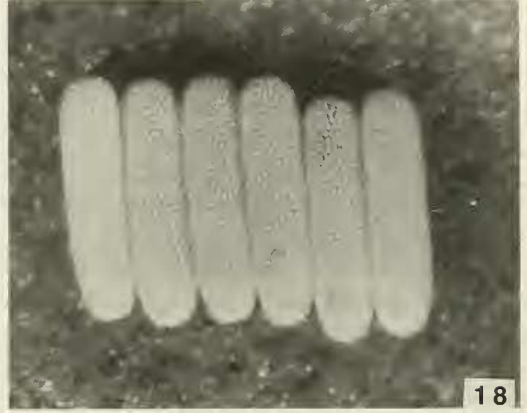
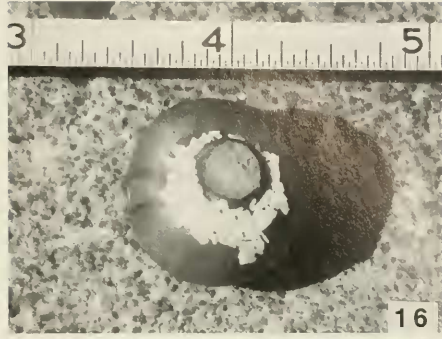


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Figs. 13–14. 13, Total number of *Notiphila* on expanded flowers of *Nuphar luteum* at the Route 43 marsh during 1992. 14, Number of males of *Notiphila* on flower buds of *Nuphar luteum* at the Route 43 marsh during 1992.



Figs. 15–20. 15, Aggregation of males of *Notiphila nudipes* on flowers of *Nuphar luteum*. 16, Eggs of *Notiphila* sp. on the underside of flower bud of *Nuphar luteum*. 17, Eggs of *Notiphila eleomyia* on the underside of a leaf of *Nuphar luteum*. 18, Close-up of *Notiphila eleomyia*. 19, Spiracular spine of larva of *Notiphila* sp. 20, Puparium of *Notiphila* sp. attached to primary root of *Nuphar*.

males collected on buds were of this species).

Mating.—Mating activity was observed in two pairs of adults of *N. eleomyia* on two flower buds that also supported several other males. Each flower bud also had 60–90 *Notiphila* eggs. In the first pair, mating lasted for six minutes. After initial copulation was completed, the male continued to ride the female for another six and a half minutes and then re-initiated copulation, remaining in copula for an additional two minutes. The female terminated copulation by pushing at the male with her hind legs. She remained on the bud, whereas the male flew away. In the second pair, copulation lasted four and a half minutes. The male then continued to ride the female for another 12 minutes before decamping.

Copulating females frequently moved about on the surface of the leaves while feeding on the accumulated honeydew. They commonly carried the male with them as they moved to the flowers for oviposition.

Oviposition.—The egg masses consisted of as few as six to a maximum of 615 eggs. Most of the egg masses were deposited primarily on the reproductive parts of *Nuphar*, although a few were found on leaves. Less than one percent of 300 leaves examined weekly along the transect possessed egg clusters, whereas over 96% of the examined flowers supported egg masses (Table 4). In large egg masses on buds, flowers, and fruits, eggs were deposited on all surfaces of these reproductive parts and frequently consisted of two or three layers. In contrast, masses deposited on leaves were always on the lower side of the leaf and usually consisted of only one layer of eggs.

The number of eggs laid per female during any one time interval varied from species to species. Females seemingly matured and deposited a full complement of eggs at one time. Two field-collected females of *N. eleomyia* deposited clusters of 25 and 27 eggs, respectively, over 24 hours in a breeding jar, suggesting that 12–14 eggs were be-

Table 4. Number of leaves and flowers of *Nuphar luteum* having eggs of *Notiphila*.

Week	Number of Leaves Examined	Number of Leaves With Eggs	Number of Flowers Examined	Number of Flowers With Eggs
24	300	0	*	*
25	300	0	*	*
26	300	6	*	*
27	300	1	*	*
28	300	3	18	18
29	300	0	6	6
30	300	1	10	9
31	*	*	10	8
32	*	*	10	10
33	*	*	10	10
34	*	*	10	10
35	*	*	8	8
36	*	*	7	6

* Not sampled.

ing released from each ovary. The ovaries of two dissected gravid females of *N. eleomyia* each consisted of 14 ovarioles. Each ovariole contained two fully formed eggs plus several others that were still undergoing oogenesis. In contrast, only six to eight ovarioles were found in each ovary of five dissected *N. nudipes*.

Eggs of both *N. eleomyia* and *N. nudipes* are white in color, show distinct texturing on the upper surface (Fig. 18), and are smooth on their ventral side. A distinct line separates the two areas. The textured dorsal surface of the egg may serve as a plastron that allows respiration to continue even when eggs are immersed in water (Hinton 1953, 1968; Deonier et al., 1978). Van der Weld and Brock (1980) demonstrated that eggs of *N. brunnipes* Robineau-Desvoidy, an European species, developed normally and hatched when submerged in well-aerated water. The incubation period for eggs of *N. eleomyia* and *N. nudipes* was three to four days. A longitudinal line of weakness at the micropylar end of the egg split open at the time of hatching, allowing the larva to emerge.

The only observed enemy of the eggs was an undetermined species of Trichogrammatidae (Hymenoptera). Every egg of

a cluster of 300 located on a *Nuphar* leaf was parasitized by this wasp.

LARVAL BEHAVIOR

Newly hatched larvae dropped from the egg masses and moved into the anaerobic sediments surrounding the roots of *Nuphar*. They fed on these sediments during the summer and fall, usually attaining the third instar before overwintering. Feeding resumed the following spring, and larvae attached themselves to the *Nuphar* roots in May (Fig. 19). The puparia were firmly affixed to the roots (Figs. 20, 21) throughout the pupal period, which lasted 14–25 days. *Notiphila bella* appeared to be univoltine, and was the first species to emerge as adults (third week of May). No adults of this species were collected after the third week of June. The remaining three species may be multivoltine, although the data are inconclusive. One possible indication of a multivoltine habit was the discovery of eight adults of *N. eleomyia* on October 8, 1992, whose ptilina were still exposed. All of these species emerged later (early June) than *N. bella* and were present in the marshes over a longer period, with adults of three species being encountered as late as early October. *Notiphila* populations peaked in late June and steadily declined as summer progressed.

DISCUSSION

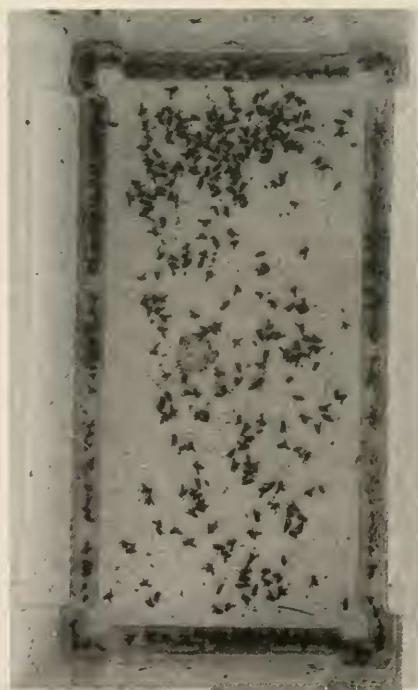
There is little evidence that competition was an important factor among the five species of *Notiphila* that dominated the *Nuphar* guild, and resource partitioning was not overly apparent. One possible example of partitioning was the fact that *N. bella* was univoltine and emerged earlier than the other four species. The two species that formed male aggregations preferred different sites, as males of *N. nudipes* formed aggregations on open flowers, whereas those of *N. eleomyia* aggregated on flower buds. Larvae of all five species co-occurred within the anaerobic sediments and apparently fed on the organic detritus. They all attached them-

selves to roots of *Nuphar* before forming puparia.

The huge number of adults obtained in the pan traps (Fig. 22) strongly suggests that the various species of *Notiphila* comprising the *Nuphar*-associated guild experience ecological release and thus can attain very large populations. We encountered very few other insect larvae in the anaerobic sediments that could be competing for the same food resource with *Notiphila*, and predators were rarely encountered.

There is a strong correlation of the life cycle of the *Nuphar*-associated species of *Notiphila* with the time of maximum oxygen richness in the roots of the water lily. Movement of oxygen from the leaves to the stems and into the roots involves diffusion and mass transport of gases driven by photosynthesis occurring in the aerial portions of *Nuphar*. Oxygenation of the rhizome and associated roots is particularly apparent in the spring when newly formed leaves are beginning to appear (Dacey 1981). This ensures that the developing pupae have access to a rich source of oxygen at a time when demand is particularly high.

An interesting question concerning *Notiphila* is why the genus is so speciose? It is the second largest genus of Ephydriidae in North America (53 spp.) being exceeded only by the phytophagous genus *Hydrellia* (60 spp.) (Wirth et al. 1987, Mathis and Zwartnicki 1995). There is a general feeling among systematists that genera comprised of plant-feeding taxa are more speciose than genera composed of predators or scavengers (Mitter et al. 1988). Speciation in phytophagous insects apparently occurred as populations shifted to new host plants and gradually adapted to the particular set of environmental conditions presented by the different host taxa. The large genus *Hydrellia* is composed of leaf-mining and stem-boring species and thus follows the expected pattern. On the other hand, species of *Notiphila* are basically detritivores, feeding on anaerobic sediments in wetland habitats. What could have driven such prolific



Figs. 21–22. 21, Respiratory spines of puparium of *Notiphila* sp. embedded in primary root of *Nuphar luteum*. 22, Adults of *Notiphila* in detergent in water pan trap collected over a 24-hour period.

Table 5. Known "host plants" of North American species of *Notiphila*.

<i>Notiphila</i> Species	Host Plant Genus	Source
The <i>adusta</i> group		
<i>N. bella</i>	<i>Nuphar</i>	This paper
<i>N. kentensis</i>	<i>Nuphar</i>	This paper
<i>N. mathisi</i>	<i>Nuphar</i>	Hurn 1984
<i>N. nudipes</i>	<i>Nuphar</i>	This paper
<i>N. taenia</i>	<i>Nuphar</i>	This paper
<i>N. theonae</i>	<i>Nuphar</i>	Hurn 1987
The <i>loewi</i> group		
<i>N. carinata</i>	<i>Justicia</i>	Deonier et al. 1978
<i>N. eleomyia</i>	<i>Nuphar</i>	This paper
<i>N. loewi</i>	<i>Potamogeton</i>	Berg 1950
<i>N. paouroua</i>	<i>Nuphar</i>	This paper
<i>N. poliosoma</i>	<i>Potamogeton</i>	Mathis 1979
<i>N. shewelli</i>	<i>Nuphar</i>	Mathis 1979
<i>N. solita</i>	<i>Typha</i>	Busacca & Foote 1978
The <i>pulchrifrons</i> group		
<i>N. scoliochaeta</i>	<i>Carex</i>	Mathis 1979
The <i>bispinosa</i> group		
<i>N. bispinosa</i>	<i>Spartina</i>	Foote, pers. obs.
<i>N. furcata</i>	<i>Spartina</i>	Foote, pers. obs.
The <i>scalaris</i> group		
<i>N. aenigma</i>	<i>Typha</i>	Busacca & Foote 1978
<i>N. decoris</i>	<i>Glyceria</i>	Foote, pers. obs.
<i>N. macrochaeta</i>	"Grasses"	Mathis 1979
<i>N. olivacea</i>	<i>Nuphar</i>	This paper
<i>N. quadrisetosa</i>	<i>Agrostis</i>	Mathis 1979
<i>N. scalaris</i>	<i>Leersia</i>	Foote, pers. obs.

speciation in this genus? We suggest that speciation occurred as populations within species of *Notiphila* adapted to different wetland plants as sources of oxygen. All species of *Notiphila*, except for those of the *caudata* group of the subgenus *Dichaeta*, are thought to obtain their oxygen from aerenchymatous tissue in the roots of wetland plants. As Table 5 shows, 22 species of *Notiphila* occurring in North America have known "host plants", although the plant associations of 31 species are still un-

known. Generalizations about suggested plant-insect relationships within the genus thus must be very tentative. The plants utilized by the five species of the *avia* group are completely unknown, and only one of the three species comprising the *pulchrifrons* group has a suspected host plant. One generalization solidly supported by evidence is that species of Monocotyledonae are preferred over species of Dicotyledonae. Only *N. carinata*, has been reported from a species of dicot (*Justicia americana* (L.) Vahl), whereas 21 species have been associated with monocots. Another well-supported generalization is that the genus *Nuphar* is heavily used by *Notiphila* larvae. At least 10 species of three different species groups representing both subgenera are known, or suspected, to attach their puparia to roots of species of yellow water lily. The *adusta* species group may be restricted to *Nuphar*, as six of its 11 species are considered to be affiliated with yellow water lilies. Finally, species of the *furcata* and *scalaris* species groups seem to show a preference for species of grasses, as six of the 19 species in those groups are known to utilize Gramineae. An interesting divergence from the typical *Notiphila* feeding pattern is possessed by species of the *caudata* group, as larvae of the only reared species, *N. dichchaeta*, feed on surface sediments and do not possess spiracular spines.

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